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Refugia under threat: mass bleaching of coral assemblages in high-latitude eastern Australia

Running head: Coral bleaching in high-latitude Australia

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Abstract

Environmental anomalies that trigger adverse physiological responses and mortality are occurring with increasing frequency due to climate change. At species' range peripheries, environmental anomalies are particularly concerning because species often exist at their environmental tolerance limits and may not be able to migrate to escape unfavourable

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conditions. Here, we investigated the bleaching response and mortality of 14 coral genera across high-latitude eastern Australia during a global heat stress event in 2016. We evaluated whether the severity of assemblage-scale and genus-level bleaching responses was associated with cumulative heat stress and/or local environmental history, including long-term mean temperatures during the hottest month of each year (SST_{LTMAX}), and annual fluctuations in water temperature (SST_{VAR}) and solar irradiance ($PARZ_{VAR}$). The most severely-bleached genera included species that were either endemic to the region (*Pocillopora aliciae*) or rare in the tropics (e.g. *Porites heronensis*). *Pocillopora* spp., in particular, showed high rates of immediate mortality. Bleaching severity of *Pocillopora* was high where SST_{LTMAX} was low or $PARZ_{VAR}$ was high, whereas bleaching severity of *Porites* was directly associated with cumulative heat stress. While many tropical *Acropora* species are extremely vulnerable to bleaching, the *Acropora* species common at high latitudes, such as *A. glauca* and *A. solitaryensis*, showed little incidence of bleaching and immediate mortality. Two other regionally-abundant genera, *Goniastrea* and *Turbinaria*, were also largely unaffected by the thermal anomaly. The severity of assemblage-scale bleaching responses was poorly explained by the environmental parameters we examined. Instead, the severity of assemblage-scale bleaching was associated with local differences in species abundance and taxon-specific bleaching responses. The marked taxonomic disparity in bleaching severity, coupled with high mortality of high-latitude endemics, point to climate-driven simplification of assemblage structures and progressive homogenisation of reef functions at these high-latitude locations.

1 | INTRODUCTION

The distribution of global biodiversity is undergoing substantial modifications as climate change accelerates and environmental anomalies become more frequent and severe (Butchart et al., 2010; Cheung et al., 2009; Parmesan & Yohe, 2003; Sala et al., 2000). One such climate-driven reconfiguration of global biodiversity during interglacial periods is linked to the propensity for cold-adapted species to migrate further toward the poles or to contract their distributions to range cores and for warm-adapted species to move toward range peripheries or to pursue *ex situ* refugia. This phenomenon, also termed 'tropicalisation' of high-latitude communities, is prevalent in both geological (Gavin et al., 2014; Greenstein & Pandolfi, 2008; Stewart, Lister, Barnes, & Dalen, 2010) and contemporary records (Chen, Hill, Ohlemuller, Roy, & Thomas, 2011; Parmesan & Yohe, 2003; Vergés et al., 2019; Wernberg et al., 2016), highlighting the significance of high-latitude regions in the persistence of many species under climate change. Interestingly, introduction of tropical species into high-latitude communities is not the only driver of contemporary changes in high-latitude community

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compositions. Climate-mediated changes in species interactions following the introduction of vagrant species into high-latitude communities (Kumagai et al., 2018; Smale et al., 2019; Vergés et al., 2019; Visser, 2008) and local rearrangements of species abundance (Tuckett, de Bettignies, Fromont, & Wernberg, 2017) can outweigh the direct influence of species range shifts on the changes in contemporary high-latitude community compositions. As such, understanding of the direct effects of progressive warming (e.g. gradual influx of tropical species), as well as the indirect effects of climate-mediated changes in species interactions and niche availability (e.g. the persistence and proliferation of resident high-latitude species) is fundamental to predicting changes in high-latitude communities.

While the tropicalisation of high-latitude communities is primarily driven by the direct and indirect effects of progressive warming, acute thermal anomalies impose punctuated stress events that further alter the dynamics of resident high-latitude species (Smale et al., 2019). A common trend observed among high-latitude marine communities under progressive warming is a regime shift in foundation species from cold-adapted macroalgae to scleractinian corals (Kumagai et al., 2018; Smale et al., 2019; Vergés et al., 2014; 2019). Notwithstanding their increasing abundances, scleractinian corals at high-latitudes are also vulnerable to acute heat stress. Similar to tropical corals, high-latitude corals suffer coral bleaching under thermal conditions that exceed long-term local averages (Celliers & Schleyer, 2002; Cook, Logan, Ward, Luckhurst, & Berg, 1990; Dalton & Carroll, 2011). The impacts of bleaching in the tropics have been well-documented over the past three decades, and recent increases in the frequency of mass bleaching events have caused large-scale mortality among corals on tropical reefs (Hughes et al., 2017). While high-latitude coral assemblages along the coasts of Australia, the Atlantic, Japan, and South Africa have also experienced varying degrees of bleaching in previous years, the overall frequency of mass bleaching events has been considerably lower than in the tropics (Abdo, Bellchambers, & Evans, 2012; Celliers & Schleyer, 2002; Cook et al., 1990; Dalton & Carroll, 2011; Harrison, Dalton, & Carroll, 2011; Hongo & Yamano, 2013; Loya et al., 2001; Schleyer, Kruger, & Celliers, 2008).

Similar to tropical reefs (Hughes et al., 2018b), bleaching at high-latitudes is characterised by taxonomic differences in bleaching susceptibility and mortality, which can lead to changes in assemblage structure (Dalton & Carroll, 2011; Floros et al., 2004; Hongo & Yamano, 2013; Loya et al., 2001). Unfortunately, high-latitude regions are predicted to experience greater

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heat stress than the tropics over the coming decades (Hobday & Pecl, 2013; Wu et al., 2012), which is likely to result in increasingly frequent and intense regional bleaching events (Heron, Maynard, van Hooidonk, & Eakin, 2016; van Hooidonk, Maynard, & Planes, 2013; van Hooidonk et al., 2016). However, unlike their tropical counterparts, poleward range shifts and/or expansions are unlikely for many high-latitude coral species because suitable habitats are progressively unavailable toward the poles, such as in the high-latitude east coast of Australia and South Africa (Harriott & Banks, 2002; Schleyer et al. 2018; but see Booth & Sears, 2018; Greenstein & Pandolfi, 2008; Richards et al., 2016). Similar to other flora and fauna (Jablonski, 2008; Parmesan, 2006), many high-latitude corals may therefore contract their geographic ranges and be more prone to extinction as their habitats become unsuitable under climate change and/or they are unable to compete with incoming vagrant species. Understanding the effects of punctuated stress events (e.g. thermal anomalies leading to bleaching) on high-latitude coral assemblages provides critical insights into the emerging changes in high-latitude community configurations over the coming decades.

In this study, we focus on the scleractinian coral assemblages of high-latitude coastal eastern Australia that harbour diverse yet spatially patchy coral assemblages (Dalton & Roff, 2013; Harriott & Banks, 2002; Sommer et al., 2017). These assemblages are inhabited by a subset of species from the nearby, tropical Great Barrier Reef (GBR) to the north, and by subtropical specialists that are either rare in the tropics or endemic to the region (Baird, Hoogenboom, & Huang, 2017; Schmidt-Roach, Miller, & Andreakis, 2013; Veron, 2000). These coral assemblages are increasingly susceptible to environmental stress as bleaching and disease outbreaks are becoming more common under climate change (Dalton & Carroll, 2011; Dalton, Godwin, Smith, & Pereg, 2010). During one of the harshest heat stress events recorded in the region, the northern and central GBR suffered severe bleaching in 2016 (Hughes et al., 2017). Here, we assess the impact of this heat stress event on the high-latitude coral assemblages across 22 locations extending south of the GBR. Specifically, we investigate the relative contributions of cumulative heat stress and local environmental history to the severity of assemblage-scale and taxon-specific bleaching responses. Further, we quantify the importance of taxonomic composition to assemblage-scale bleaching severity measurements. Lastly, we discuss how taxonomic variability in bleaching vulnerability and immediate mortality, coupled with geographic patterns in species composition, may lead to a reorganisation of high-latitude coral assemblages. Together, the findings from this study improve our knowledge of the vulnerability of high-latitude corals under climate change.

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2 | MATERIALS AND METHODS

2.1 | Bleaching surveys and response metrics

We surveyed a total of 8,952 coral colonies across 22 sites along the subtropical east coast of Australia spanning 26°S to 31°S (Fig. 1) between April and May 2016, using rapid underwater assessment methods described below. The timing of our April survey coincided with the peak of heat stress at 19 of the survey sites. Three additional sites (Black Rock, Cook Island, and Julian Rocks) were surveyed in May, within six weeks of maximum heat stress. At each site, a 1 m^2 quadrat was placed every 5 m along three or four 25 m belt transects, laid at a depth between 3 and 13 m depending on the topography and depth profile of each location. In each quadrat, all coral colonies were identified to the genus level. Recent changes to the nomenclature of regional species (Table S1) included divisions and synonymy of a few genera (Arrigoni et al., 2016; Budd, Fukami, Smith, & Knowlton, 2012; Huang, Benzoni, Arrigoni, et al., 2014a; Huang, Benzoni, Fukami, et al., 2014b). Members of the synonymised genera showed minimal bleaching severity and no immediate mortality, suggesting negligible impact of taxonomic updates on bleaching patterns found among the synonymised genera (Table S2). The health of each colony was visibly assessed *in situ* and scored as a categorical variable with five levels: (0) no visible bleaching, (1) 1-20% of the colony bleached, (2) 21-50% bleached, (3) 51-80% bleached, and (4) 81-100% bleached. Pigmentation patterns of a coral can differ depending on environmental conditions and location (Brown, Dunne, Ambarsari, Le Tissier, & Satapoomin, 1999; Fitt, McFarland, Warner, & Chilcoat, 2000; Wallace, Fellegara, Muir, & Harrison, 2009). Therefore, signs of pigmentation, such as a mottled or pale appearance, were not included in the bleaching severity measurements, providing a conservative estimate of bleaching responses. Coral colonies were scored as 'recently dead' (i.e. immediate post-bleaching mortality) when live tissue was lost completely from the skeleton and an initial colonisation of turf algae was evident.

The severity of the bleaching response for each coral genus was calculated for each survey replicate as the weighted mean of the five health assessment categories (0-4, detailed above), adjusted by the proportion of coral colonies in each category (i.e. bleaching index – measure of taxon-specific bleaching response; modified from McClanahan, Baird, Marshall, & Toscano, 2004; Eq. 1);

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$$Bleaching\ index\ (BI) = \frac{1}{n-1}\sum_{i=0}^{n-1}\left(\frac{i\ *\ x_i}{X}\right), where\ X = \sum_{i=0}^{n-1} x_i \quad \text{(Eq. 1)}$$

where n is the number of health assessment categories (n = 5 in this study), with an increase in the category value (i) indicating an increase in bleaching severity, and x_i is the number of coral colonies in the i^{th} category. A bleaching index value of 0 indicates none of the colonies are affected by bleaching, and a value of 1 indicates that all colonies within a genus were affected under the highest severity category. To obtain an estimate of site-level bleaching severity, we used the site susceptibility index (SSI – measure of assemblage-scale bleaching response) that considers the regional BI of each genus and weights the relative abundance of each genus present at a specific site (modified from McClanahan et al., 2007b; Eq. 2);

$$Site\ susceptibility\ index\ (SSI) = \sum_{i=1}^{n}\frac{(\mu_{BI_i} * x_i) * 100}{X}, where\ X = \sum_{i=1}^{n} x_i \quad \text{(Eq. 2)}$$

where n is the number of taxa (i.e. genera) present at a site, $\mu_{BI_i}$is the mean bleaching index for the i^{th} taxon across the region, and x_i is the number of coral colonies for the i^{th} genus at the site. Unlike the bleaching index, the site susceptibility index does not have a maximum positive value limit. Higher SSI values indicate higher assemblage-scale susceptibility, and 0 SSI suggests no colonies at the site were affected, irrespective of the taxonomic composition of the assemblage.

2.2 | Environmental data

To examine the effects of local-scale variability in cumulative heat stress and of long-term environmental parameters on assemblage-scale and taxon-specific bleaching responses, we compiled a suite of remote sensing satellite data. The Degree Heating Week (DHW) metric was used as a measure of heat stress and calculated using version 3.1 of the NOAA Coral Reef Watch dataset at 5 km spatial resolution (Liu et al., 2014). The conventional DHW metric accumulates SST anomalies exceeding 1°C above the long-term maximum of the monthly mean (MMM) climatology (hereafter DHW_{1C}). To assess the potential effect of low-magnitude heat stress, we also computed DHW with the same MMM climatology, but without the 1°C filter (hereafter DHW_{0C}; van Hooidonk & Huber, 2009). For any given heat stress event, DHW_{0C} is greater than DHW_{1C} as it includes contributions when SST exceeds the MMM by less than 1°C. We compared temperature measurements between remote sensing satellite and *in situ* logger data (present at seven sites) to assess the robustness of our heat stress measurements and long-term environmental parameters obtained from satellite

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data. Our analysis showed that the satellite data provided robust approximations of *in situ* thermal conditions (site-specific Pearson's correlation coefficients between satellite and logger were between 0.88 and 0.92, with all p-values < 0.001; Fig. S1; Table S3).

Long-term environmental parameters derived from remote sensing satellite data included long-term means of the hottest month of each year, and annual variability in thermal conditions and solar irradiance. These parameters were selected based on experimental and *in situ* evidence in the literature that showed their direct influence on bleaching severity (Brown, Dunne, Goodson, & Douglas, 2002; Hoegh-Guldberg, 1999; Lesser, Stochaj, Tapley, & Shick, 1990; McClanahan, Maina, Moothien-Pillay, & Baker, 2005). Long-term mean water temperature of the hottest month of each year between 1985 and 2015 (hereafter SST_{LTMAX}) was used as a measure of the upper-bound thermal conditions at each site. Using the same sea surface temperature (SST) data, variability in thermal conditions (hereafter SST_{VAR}) was calculated as the long-term mean of the standard deviation of annual SST. Further, we calculated annual variation in solar irradiance (hereafter $PARZ_{VAR}$) as the long-term mean of the standard deviation of annual photosynthetically active radiation (PAR) between 2002 and 2015. The amount of PAR reaching the benthos decreases with depth and with increasing turbidity (Read, Rose, Winslow, & Read, 2015), and we adjusted the PAR values at each site accordingly (i.e. PARZ; Pierson, Kratzer, Strömbeck, & Håkansson, 2008; Eq. 3);

$$PARZ = PAR_0 * e^{(-K490 * Z)} \text{ (Eq. 3)}$$

where PAR_0 is PAR on the surface, $K490$ is the diffuse attenuation coefficient (a measure of turbidity), and Z is the survey depth at each site. SST_{VAR} and $PARZ_{VAR}$ are particularly relevant for high-latitude reefs because the monthly and seasonal fluctuations of these parameters are greater in high-latitude regions than most locations in the tropics (Beger, Sommer, Harrison, Smith, & Pandolfi, 2014; Malcolm, Davies, Jordan, & Smith, 2011; Sommer, Beger, Harrison, Babcock, & Pandolfi, 2018). SST_{LTMAX} and SST_{VAR} were calculated using version 3.1 of the NOAA Coral Reef Watch dataset at 5 km spatial resolution (Liu et al., 2014). PAR and K490 data were obtained from the Global Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua Satellite products at 4 km resolution (Parkinson, 2003).

2.3 | Data analyses

2.3.1 | Assemblage-scale bleaching response

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Before examining the effects of environmental parameters and taxonomic composition on assemblage-scale bleaching responses, we first checked for multicollinearity of environmental parameters using Pearson's correlation coefficient and variance inflation factor (VIF) with cut-offs of r = ±0.65 and VIF = 2, respectively (Craney & Surles, 2007; Gordon, 2015). DHW_{1C} showed a higher VIF value and larger Pearson's correlation coefficients with other environmental variables than those exhibited by DHW_{0C}. Therefore, DHW_{0C} was used in all our models (Fig. S2; Table S4). Subsequently, we evaluated a variety of variable combinations using the widely applicable information criterion (WAIC) and leave-one-out cross-validation (LOO) to select the final model (Table S5; Vehtari, Gelman, & Gabry, 2017). The final model included DHW_{0C}, SST_{LTMAX}, SST_{VAR}, and $PARZ_{VAR}$ as independent environmental parameters. VIF and model selection criteria were computed using the 'usdm' (Naimi, Hamm, Groen, Skidmore, & Toxopeus, 2014) and 'loo' (Vehtari et al., 2017) packages. All modelling and analyses in this study were conducted in R (R Core Team 2018).

We used hierarchical Bayesian generalised linear models with student's t-distribution to assess the effects of heat stress, long-term environmental parameters, and the relative abundance of each taxon in an assemblage on regional assemblage-scale (SSI) bleaching responses. To account for spatial autocorrelation stemming from geographic clustering of survey sites, survey site location was included as a random effect after categorisation into seven groups based on geographic proximity and shelf position: Inner Moreton Bay, Outer Moreton Bay, Northern New South Wales, Inshore Solitary Islands, Mid-shelf Solitary Islands, Offshore Solitary Islands, and Central New South Wales (see Table S6 for detailed site information). Models were executed in Stan (Carpenter et al., 2017) with weakly informative normal priors assigned for beta parameters and gamma priors for degrees of freedom. All Stan models were called from R using the 'rstan' package (Stan Development Team 2018). Each model was run with four chains of 20,000 iterations; the first 10,000 iterations were discarded as warm-up, and all subsequent iterations were sampled. We examined all chains for model convergence, the adequacy of warm-up, and autocorrelation (Fig. S3). The Gelman-Rubin diagnostic ($\hat{R}$) compares the variance of each chain to the compiled variance of all chains, and values under 1.001 are desirable to ensure appropriate chain convergence (Gelman & Shirley, 2011). $\hat{R}$ values for all parameters of the assemblage-scale response models were equal to or below 1. Model fits were summarised using the

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highest posterior density (HPD) interval as the credible interval, and median point estimates for all chains were computed.

2.3.2 | Taxon-specific bleaching responses

Taxonomic variability in overall bleaching severity across our survey sites was tested by comparing the bleaching index (BI) of the five most abundant genera (*Acropora*, *Goniastrea*, *Pocillopora*, *Porites*, and *Turbinaria*) using an analysis of variance (ANOVA) and Tukey's post-hoc test. We also used generalised additive models (GAM) to test whether the taxon-specific BI was linked to the relative proportion of 'recently dead' colonies (i.e. immediate mortality). *Goniastrea* and *Turbinaria* were excluded from the mortality analysis as they suffered no or negligible mortality (*Goniastrea*: no mortality; *Turbinaria*: one colony mortality across all survey sites). GAMs were run using the 'mgcv' package in 'R' (Wood, 2011).

The influence of heat stress and long-term environmental parameters on the taxon-specific bleaching index (BI) was examined using a hierarchical Bayesian beta regression model with logit link. The taxon-specific response model was restricted to the same five most abundant genera and executed in Stan (Carpenter et al., 2017), with weakly informative normal priors assigned for beta parameters and gamma priors for the dispersion parameter. In addition to the geographic group random effect in the assemblage-scale models (Table S6), survey site locations were included as a second random effect nested in geographic group to account for survey replicates within the same site. The taxon-specific BI values were transformed using a data range compression method (Smithson & Verkuilen, 2006) to preserve crucial information in zero (no bleaching) values. The taxon-specific response model was run with the same number of chains, iterations, and warm-up as the assemblage-scale response models (model diagnostics – Fig. S4). $\hat{R}$ values for all parameters of the taxon-specific response model were equal to or below 1.

2.3.3 | Inferring Bayesian results

Estimated model coefficients (β coefficients) indicate the modelled effect of a given predictor on bleaching severity. Positive and negative β coefficients suggest corresponding strength of positive or negative correlation between a given predictor variable (environmental parameter, relative abundance of taxa) and the response variable (bleaching severity). The HPD intervals

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reflect the distribution of β coefficients (i.e. distribution of modelled effects of a predictor on bleaching severity) that is supported by the data. A high precision of β coefficients leads to a high probability density and narrow posterior distribution of β coefficients, whereas low precision of β coefficients results in low probability density and wide posterior distribution of β coefficients.

2.3.4 | Spatial patterns of coral bleaching impacts

To examine spatial patterns of taxon-specific bleaching severity and their subsequent impacts on local assemblage structures, we examined the correlation between taxon-specific bleaching severity of the five most abundant genera and latitude, as well as the correlation between their relative abundances and latitude using Pearson's correlation coefficient. The Coffs Harbour region has the most extensive high-latitude coral assemblages along the east coast of Australia, whereas assemblages elsewhere in the region are generally more patchy in their distribution with considerably lower coral cover (Fig. 1; Dalton & Roff, 2013; Harriott, Smith, & Harrison, 1994; Harriott & Banks, 2002). To examine whether the disproportionate concentration of survey sites near Coffs Harbour skewed spatial patterns of bleaching severity and assemblage compositions, we conducted a sensitivity test. A random number of survey replicates were selected from the survey sites near Coffs Harbour and were combined with survey replicates from other sites. Subsequently, these combined site datasets were used to test correlations between taxon-specific bleaching index (BI) of the five most abundant genera and latitude, as well as their relative abundances and latitude. This process was repeated 1,000 times and summary statistics of the iterations were used to infer statistical significance of the correlations between taxon-specific bleaching severity and latitude, and between relative abundance and latitude.

3 | RESULTS

3.1 | Assemblage-scale bleaching response

The environmental parameters explored here did not capture the observed differences in assemblage-scale bleaching severity (Site susceptibility index – SSI; Fig. 2a; Table S7). In particular, estimated model coefficients for all environmental parameters were centred near zero with wide posterior density intervals, indicating that these parameters were poorly associated with the patterns of assemblage-scale bleaching responses. Model residuals also showed no gradient pattern between all bivariate environmental variable combinations,

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indicating that two-way interactive effects between tested environmental variables also were unrelated to assemblage-scale bleaching severity (Fig. S5). In contrast, the variation in taxonomic composition among assemblages was linked to the site susceptibility index (SSI). The relative abundance of *Pocillopora,* in particular, was strongly associated with SSI (Fig. 2b; Table S8). SSI was higher at sites where *Pocillopora* was more abundant. Posterior density intervals of β coefficients for other genera, including regionally common *Acropora*, *Goniastrea*, *Porites*, and *Turbinaria*, were wide and crossed zero, indicating an unlikely association between the relative abundance of these genera and assemblage-scale bleaching severity.

3.2 | Taxon-specific bleaching responses

Taxon-specific bleaching severity and immediate mortality were strikingly different among the five most abundant genera (Fig. 3; Table S9; Table S10). Among the five most abundant genera, *Pocillopora* and *Porites* were significantly more susceptible to bleaching than *Acropora*, *Goniastrea*, and *Turbinaria* (Fig. 3a; Table S9). Despite the similarity in the bleaching index (BI) values of the two severely impacted genera, they differed in patterns of mortality; mortality rose as BI increased for *Pocillopora*, whereas mortality and BI were not correlated for *Porites* (Fig. 3d; Fig. 3e; Table S10). *Acropora*, *Goniastrea*, and *Turbinaria* also had similar degrees of bleaching to one another, and exhibited little or no bleaching (Fig. 3a; Table S9) or mortality (Fig. 3b; Fig. 3c; Fig. 3f; Table S10).

The taxon-specific bleaching severity (BI) was associated with environmental predictors, yet the specific predictors that affected bleaching severity responses differed among genera (Fig. 4; Table S11). Bleaching worsened with increasing heat stress (DHW) for *Porites* (Fig. 4a), whereas *Pocillopora* bleached more at sites where water temperature was historically cooler (SST_{LTMAX}; Fig. 4b), or experienced higher fluctuations in annual solar irradiance ($PARZ_{VAR}$; Fig. 4d). The bleaching severities of *Pocillopora* and *Porites* were not linked to the annual variation in historical water temperature (SST_{VAR}; Fig. 4c). Contrary to the clear associations between bleaching severity and environmental parameters found among *Pocillopora* and *Porites*, bleaching severities of *Acropora*, *Goniastrea*, and *Turbinaria* were not correlated with any of the examined environmental parameters. Overall absolute model residuals were low for *Acropora*, *Goniastrea*, and *Turbinaria,* whereas *Pocillopora* and *Porites* showed

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considerably higher absolute model residuals without a notable pattern between all bivariate environmental variable combinations (Figure S6).

3.3 | Spatial patterns of bleaching severity

The geographic pattern in bleaching severity (BI) and the relative effect of bleaching on local populations differed among genera (Fig. 5; Fig. S7; Fig. S8; Table S12). Overall, the severity of bleaching response for the genus *Acropora* was minimal and did not vary across latitude (Table S12; mean r = -0.26, R^2 = 0.07, p = 0.12), while the relative proportion of *Acropora* in assemblages declined toward higher latitudes (Fig. 5a; mean r = -0.55, R^2 = 0.3, $p < 0.01$). Bleaching severity of *Goniastrea* declined toward higher latitudes (Fig. 5b; mean r = -0.54, R^2 = 0.29, $p < 0.01$), without a corresponding change in relative abundance (Fig. 5a). Bleaching was also less severe for *Turbinaria* toward higher latitudes (Fig. 5d; mean r = -0.46, R^2 = 0.21, $p < 0.01$), yet its relative contribution to the total species assemblage increased with latitude (Fig. 5a; mean r = 0.56, R^2 = 0.32, $p < 0.01$). In contrast, bleaching severity for *Pocillopora* increased with latitude (Fig. 5c; mean r = 0.51, R^2 = 0.27, $p < 0.01$), without a significant change in its relative abundance across latitude (Fig. 5a; mean r = 0.23, R^2 = 0.06, p = 0.12). There was no correlation between bleaching severity (Table S12; mean r = 0.002, R^2 = 0.004, p = 0.85) or relative abundance and latitude for *Porites* (Fig. 5a; mean r = 0.32, R^2 = 0.12, p = 0.08).

4 | DISCUSSION

Analysis of the spatial and taxonomic patterns of coral bleaching allows us to identify specific coral taxa or assemblages vulnerable to climate change and to predict future configurations of coral assemblages (Hughes et al., 2018a; 2018b; Loya et al., 2001; van Woesik, Sakai, Ganase, & Loya, 2011). Our findings highlight that in high-latitude eastern Australia, assemblage-scale patterns of coral bleaching are heavily influenced by local abundance of a regionally common genus sensitive to heat stress, *Pocillopora*, instead of environmental gradients. Further, the clear distinction in taxon-specific bleaching severity and immediate mortality, coupled with spatial patterns of taxon-specific bleaching responses and abundances, may lead to simplification of assemblage structures and gradual homogenisation of reef functions.

4.1 | The importance of taxonomic composition in assemblage-scale bleaching responses

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Bleaching among the high-latitude coral assemblages along eastern Australia was initiated by record heat stress in early 2016 (Fig. S9). Nevertheless, regional variability in the severity of assemblage-scale bleaching responses (SSI – site susceptibility index) was poorly explained by cumulative heat stress (Degree Heating Weeks) and long-term environmental conditions. While remote sensing satellite data provided robust estimates of the regional variation in water temperature (Fig. S1; Table S3), they were unlikely to capture fine temporal- and spatial-scale variation in environmental conditions due to their coarser measurement scales than *in situ* loggers (e.g. Castillo & Lima, 2010). It is plausible that these fine temporal- and spatial-scale environmental parameters might include predictors that are better able to explain the observed patterns of assemblage-scale bleaching severity, such as local high-frequency temperature variability (Safaie et al., 2018).

Interestingly, the severity of assemblage-scale bleaching responses was associated with the relative abundance of *Pocillopora*, a genus that is highly susceptible to heat stress (Fig. 3; Loya et al., 2001; Marshall & Baird, 2000; McClanahan et al., 2004; van Woesik et al., 2011). By definition, assemblage-scale bleaching metrics (e.g. SSI, Eq. 2) are influenced by both species abundances and their respective bleaching responses. Severe bleaching of a single, locally dominant species in an assemblage can produce a comparable SSI value (or an assemblage-scale percentage of bleached corals) to another assemblage where many different species experienced mild bleaching. As such, assemblage-scale metrics can be difficult to interpret or may poorly explain the bleaching dynamics for coral assemblages characterised by high variation in community structure. The close linkage between the abundance of bleaching-susceptible taxa and assemblage-scale bleaching severity thus highlights the limitations of assemblage-scale bleaching metrics and supports the idea that assessments of bleaching impact should consider spatial variation in community composition and taxon-specific (e.g. species- or genus-specific) bleaching responses (Marshall & Baird, 2000; Fitt, Brown, Warner, & Dunne, 2001; Safaie et al., 2018).

4.2 | Taxon-specific environmental drivers of bleaching severity responses

Contrary to the overall lack of association between environmental parameters and assemblage-scale bleaching severity (SSI), taxon-specific bleaching (BI) patterns for *Porites* and *Pocillopora* showed clear linkages to environmental parameters. Interestingly, *Porites* was the only genus whose bleaching severity escalated with heat stress (Fig. 4a). *Porites* species with massive growth forms are generally considered to be less sensitive to bleaching

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(Loya et al., 2001; Marshall & Baird, 2000; McClanahan et al., 2004), yet encrusting *Porites* species, such as those abundant along the high-latitude eastern Australia and at other high-latitude regions, can be vulnerable to heat stress and susceptible to bleaching (Dalton & Carroll, 2011; van Woesik et al., 2011). On the other hand, patterns of bleaching severity for *Pocillopora* were best explained by long-term environmental conditions. Specifically, prior exposure to warm temperature (SST_{LTMAX}) and low variability in solar irradiance ($PARZ_{VAR}$) reduced the severity of bleaching. These patterns are consistent with previous findings, in which long-term exposure to higher temperature was linked to a reduction in acute responses to heat stress (Brown et al., 2002; Brown & Dunne, 2016; Griffin, Bhagooli, & Weil, 2006; Woolsey, Keith, Byrne, Schmidt-Roach, & Baird, 2015). A recent study on *Pocillopora* also highlighted that experimental transplantation of coral colonies from low to high fluctuations in PAR increased the sensitivity of corals to heat stress (Sampayo et al., 2016). While previous studies indicated that exposure to fluctuating water temperature might enhance thermal tolerance (McClanahan, Ateweberhan, Muhando, Maina, & Mohammed, 2007a; Woolsey et al., 2015), we found that fluctuation in annual water temperature had little effect on taxon-specific bleaching severity. This lack of correlation between fluctuation in water temperature and taxon-specific bleaching severity may be due to the narrower range of SST_{VAR} across our survey sites (< 2.4°C) compared to the previously reported experimental threshold for biological responses among regional corals (+4°C; Woolsey et al., 2015).

Patterns of bleaching severity for *Acropora*, *Goniastrea*, and *Turbinaria* were not linked to any of the explored environmental parameters. The genus *Acropora* contains numerous tropical species that tend to suffer severe bleaching and mortality during mass bleaching events (Goreau, McClanahan, Hayes, & Strong, 2000; Hughes et al., 2019; Marshall & Baird, 2000; McClanahan et al., 2004). However, our findings showed that high-latitude *Acropora* species, such as *A. glauca* and *A. solitaryensis*, were resistant to heat stress. Low sensitivity to bleaching among high-latitude *Acropora* spp. has also been reported in other parts of the globe, highlighting distinctive bleaching resilience among high-latitude members of this genus (Celliers & Schleyer, 2002; van Woesik et al., 2011; but see Hongo & Yamano, 2013). Overall, the variability in taxon-specific bleaching responses under the same environmental conditions observed across our study sites supports the notion that mild to moderate bleaching episodes can identify locally/regionally resistant (e.g. *Goniastrea*, *Turbinaria*, and high-latitude *Acropora* spp.) and vulnerable (e.g. *Pocillopora* and regional encrusting *Porites*

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spp.) taxa (Hughes et al., 2017, 2018b; Loya et al., 2001; Marshall & Baird, 2000; van Woesik et al., 2011). However, the distinction between bleaching tolerant and susceptible taxa likely varies in space and with environmental conditions, such as local environmental history and microhabitats (Safaie et al., 2018), and biological factors, including species identity, traits (Mizerek, Baird, & Madin, 2018), and the presence of locally adapted genotypes (Bay & Palumbi, 2014; LaJeunesse, Reyes-Bonilla, & Warner, 2007). Long-term studies that examine taxon-specific bleaching mechanisms over a broad spatial scale are therefore needed to understand shifts in ecosystem dynamics under climate change.

4.3 | Regional implications of taxonomic variability in bleaching impact and abundance

Against the backdrop of species migrations (Baird, Sommer, & Madin, 2012) and tropicalisation of high-latitude marine ecosystems (Smale et al., 2019; Vergés et al., 2014; 2019; Wernberg et al., 2016), taxon-specific bleaching, mortality, and spatial abundance patterns have the potential to broadly affect ecosystem structure and functioning (Hughes et al., 2003; 2018b; Pandolfi, Connolly, Marshall, & Cohen, 2011; Stuart-Smith, Brown, Ceccarelli, & Edgar, 2018). While both *Pocillopora* and *Porites* experienced severe bleaching, bleaching severity was only linked to immediate mortality of *Pocillopora* (Fig. 3d). Post-bleaching mortality data from the Solitary Islands showed that the immediate mortality pattern of *Pocillopora* observed in this study worsened, and *Pocillopora* suffered significant declines in abundance (Cant et al. 2018). In contrast, *Turbinaria* was the only genus that experienced mild bleaching, was more abundant at higher latitudes, and did not suffer severe bleaching or mortality (Fig. 3f; Cant et al. 2018). These patterns suggest that recurrent bleaching and mortality events may lead to increased dominance of *Turbinaria* and declines of *Pocillopora* on high-latitude reefs, especially if the capacity for population recovery is affected by the severity of bleaching (Hughes et al., 2019).

On tropical coral reefs, changes in assemblage composition following disturbance are largely a function of other tropical taxa filling gaps in physical space vacated by vulnerable taxa (Stuart-Smith et al., 2018). On high-latitude reefs, loss of vulnerable taxa potentially creates opportunities for thermally-resilient local/regional taxa and incoming tropical taxa that benefit from warming temperatures at high latitudes, thereby introducing new sets of life-history traits to the ecosystem (Beger et al., 2014; Greenstein & Pandolfi, 2008; Sommer et al., 2018). For example, corals on tropical coral reefs exhibit diverse growth forms and create complex three-dimensional frameworks, whereas corals on high-latitude reefs tend to have

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more uniform or less diverse morphologies (Sommer, Harrison, Beger, & Pandolfi, 2014), generally resulting in structurally less complex coral framework toward higher latitudes (DeVantier, De'Ath, Turak, Done, & Fabricius, 2006; Mizerek, Baird, Beaumont, & Madin, 2016). Therefore, loss of species in high-latitude assemblages and replacement by tropical taxa could not only lead to a change in the assemblage composition, but also result in a significant shift in habitat complexity. However, the growth of structurally complex tropical taxa at high-latitudes may be inhibited by chemical conditions increasingly less conducive to calcification with climate change (e.g. ocean acidification; van Hooidonk, Maynard, Manzello, & Planes, 2014) or by oceanographic conditions particularly unfavourable for corals with complex morphologies (e.g. strong wave actions; Harriott & Banks, 2002). Such conditions may hamper the poleward range expansion of tropical corals, in which case, the marked disparity in taxon-specific bleaching severity and mortality will likely lead to proliferation of resident bleaching-resistant corals and a homogenisation of assemblages, which in turn can impair ecosystem functioning (Clavel, Julliard, & Devictor, 2011; McKinney & Lockwood, 1999).

4.4 | Outlook and conclusion

The resilience of coral reefs to environmental anomalies is rapidly weakening as corals are exposed to extreme conditions more frequently, and their capacity to rebound is declining (Heron et al., 2016; Hughes et al. 2019; van Hooidonk et al., 2013; van Woesik et al., 2011). While high-latitude reefs have been considered as potential climate refugia for tropical corals under climate change (Beger et al., 2014; Riegl, 2003; but see Lybolt et al., 2011), our findings suggest that resident high-latitude corals are also vulnerable to thermal anomalies, potentially without suitable *ex situ* climate refugia equivalent to those of tropical corals (Harriott & Banks, 2002; Schleyer et al., 2018). The levels of heat stress measured among subtropical assemblages were relatively low (DHW_{0C} of 4-9°C-weeks) compared to those recorded in the tropics during the same time period of 2016 (up to DHW_{1C} of 12°C-weeks; Hughes et al., 2017). Nonetheless, bleaching was prevalent throughout the region and resulted in severe bleaching of two abundant genera, *Pocillopora* and *Porites*. This is particularly concerning because some representatives of these genera are endemic species (*Pocillopora aliciae* Schmidt-Roach et al., 2013) or rare in the tropics (*Porites heronensis* Veron, 1985). Loss of endemic or locally abundant taxa is more than a simple loss of biodiversity as it can undermine ecosystem processes (e.g. energy flow), deprive the

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ecosystem of novel ecological interactions (Bailey, Wooley, Lindroth, & Whitham, 2006; Gorman, Potts, Schweitzer, & Bailey, 2014; Valiente-Banuet et al., 2015), and incur a critical loss in evolutionary history for the taxonomic group (Huang & Roy, 2013; 2015). The degree of changes in the ecological functions of high-latitude coral assemblages, and the ability of high-latitude areas to act as climate refugia for tropical taxa will depend upon recovery patterns of bleaching-susceptible regional taxa, range expansion rates of tropical taxa, the relative strength of competitive advantages that resident high-latitude corals possess over the ability of tropical corals to colonise the rocky substrates in the subtropics, and the frequency and magnitude of recurrent environmental anomalies. Importantly, our mechanistic understanding of coral bleaching, and efforts to predict the future of reefs are nullified under extreme and unprecedented thermal conditions (Hughes et al., 2017), making the reduction of global warming an urgent priority.

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FIGURE CAPTIONS

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Figure 1. Survey locations along the subtropical east coast of Australia spanning 26°S to 31°S. Black dots mark the location of each survey site and red polygons indicate the known presence of coral assemblages.

Figure 2. The effects of (a) environmental variables and (b) taxonomic composition on assemblage-scale bleaching severity. Points indicate the median of the 95% highest posterior density (HPD) intervals of β coefficients, and horizontal lines indicate the 95% HPD intervals. Statistical significance is inferred where the 95% HPD interval does not intersect 0 and is annotated with a closed symbol. A positive β coefficient represents a positive association and a negative β coefficient indicates a negative association between assemblage-scale bleaching severity (SSI) and (a) an environmental variable or (b) relative abundance of a genus. The genera annotated with an asterisk have undergone a recent taxonomic revision (Table S1).

Figure 3. Intergeneric variability in (a) bleaching index (BI) and (b-f) the relationship between bleaching index (BI) and immediate mortality for *Acropora*, *Goniastrea**, *Pocillopora*, *Porites*, and *Turbinaria*. The genera in (a) are grouped based on statistical similarity in bleaching index (brackets A and B). The box plots illustrate interquartile ranges of BI for each genus, whiskers indicate minimum and maximum values not exceeding 1.5 times below and above the first and third quartiles (i.e. Tukey's boxplot) and dots indicate outliers. (b-f) Each dot represents the mean BI and immediate mortality for the taxon at each of the survey sites. Horizontal and vertical lines represent 95% confidence intervals for the mean values. Splines were estimated using generalised additive models with only significant relationships shown, and the shaded areas represent 95% confidence intervals (Table S10). Note the figures (b-f) are on different y-axis scales.

Figure 4. The effect of environmental variables on taxon-specific bleaching severity for: (a) Degree Heating Weeks (DHW_{0C}), (b) long-term mean water temperature of hottest month of each year (SST_{LTMAX}), (c) long-term mean of annual fluctuations in water temperature (SST_{VAR}), and (d) long-term mean of annual fluctuation in solar irradiance ($PARZ_{VAR}$). Points indicate the median of the 95% highest posterior density (HPD) intervals of β coefficients, and lines indicate the 95% HPD intervals. Statistical significance is annotated with a closed symbol. A positive β coefficient represents a positive association and a negative

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925 β coefficient indicates a negative association between an environmental variable and taxon-
926 specific bleaching severity (BI).
927
928 **Figure 5.** (a) The relative contribution of the five most abundant genera (*Acropora*,
929 *Goniastrea**, *Pocillopora*, *Porites*, and *Turbinaria*) and all remaining genera (Others) to
930 assemblage composition across latitude. Sites are grouped based on geographic proximity for
931 graphical purposes. Direct correlation between relative abundance and latitude can be found
932 in Table S12. (b)-(d) The bleaching index (BI) for three of the five most abundant genera
933 across latitude. Each point represents the mean BI for a survey site. Vertical lines are 95%
934 confidence intervals for the mean BI values. The slope of regressions indicates the
935 relationship between latitude and BI. Only statistically significant relationships are depicted.

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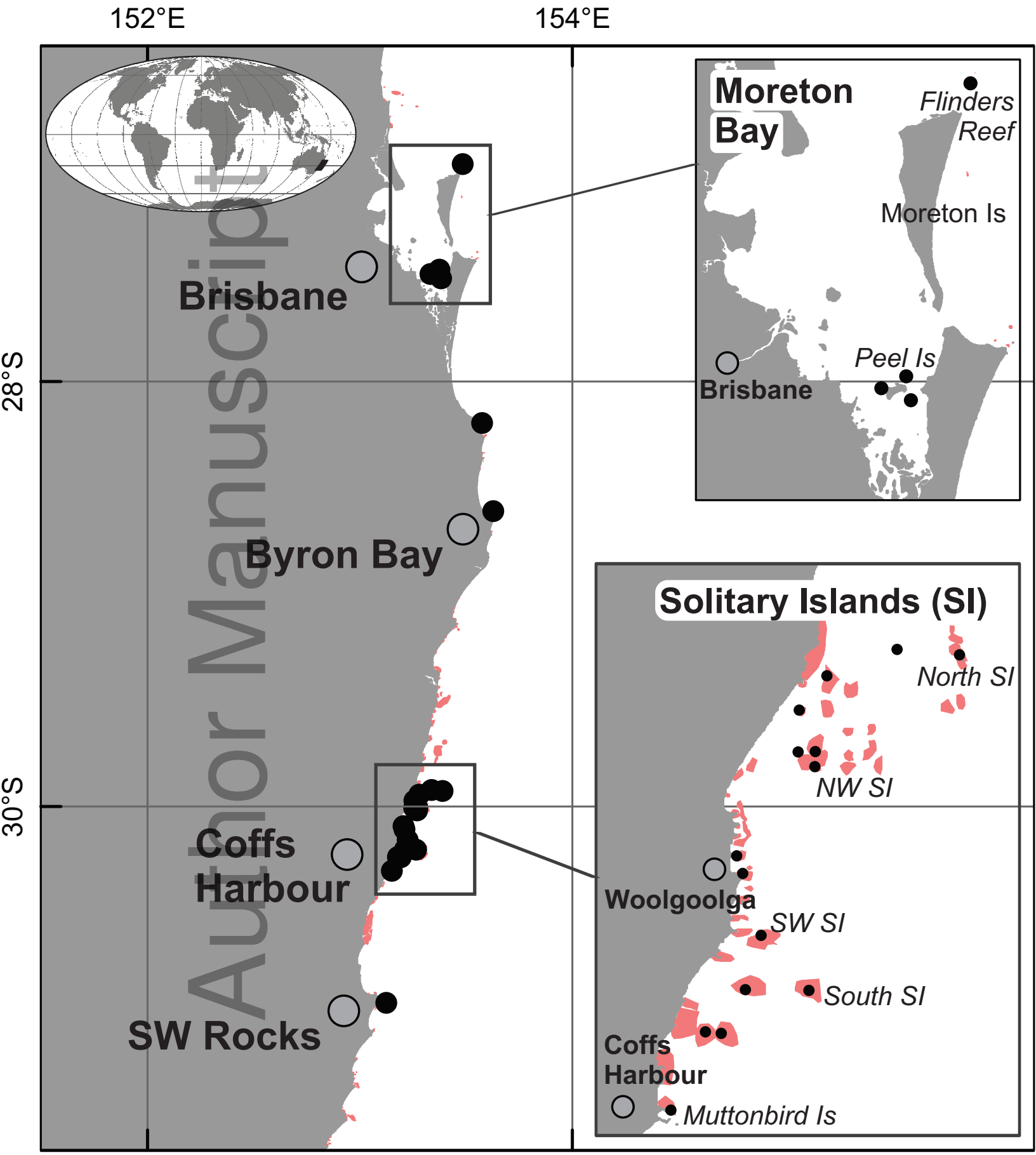

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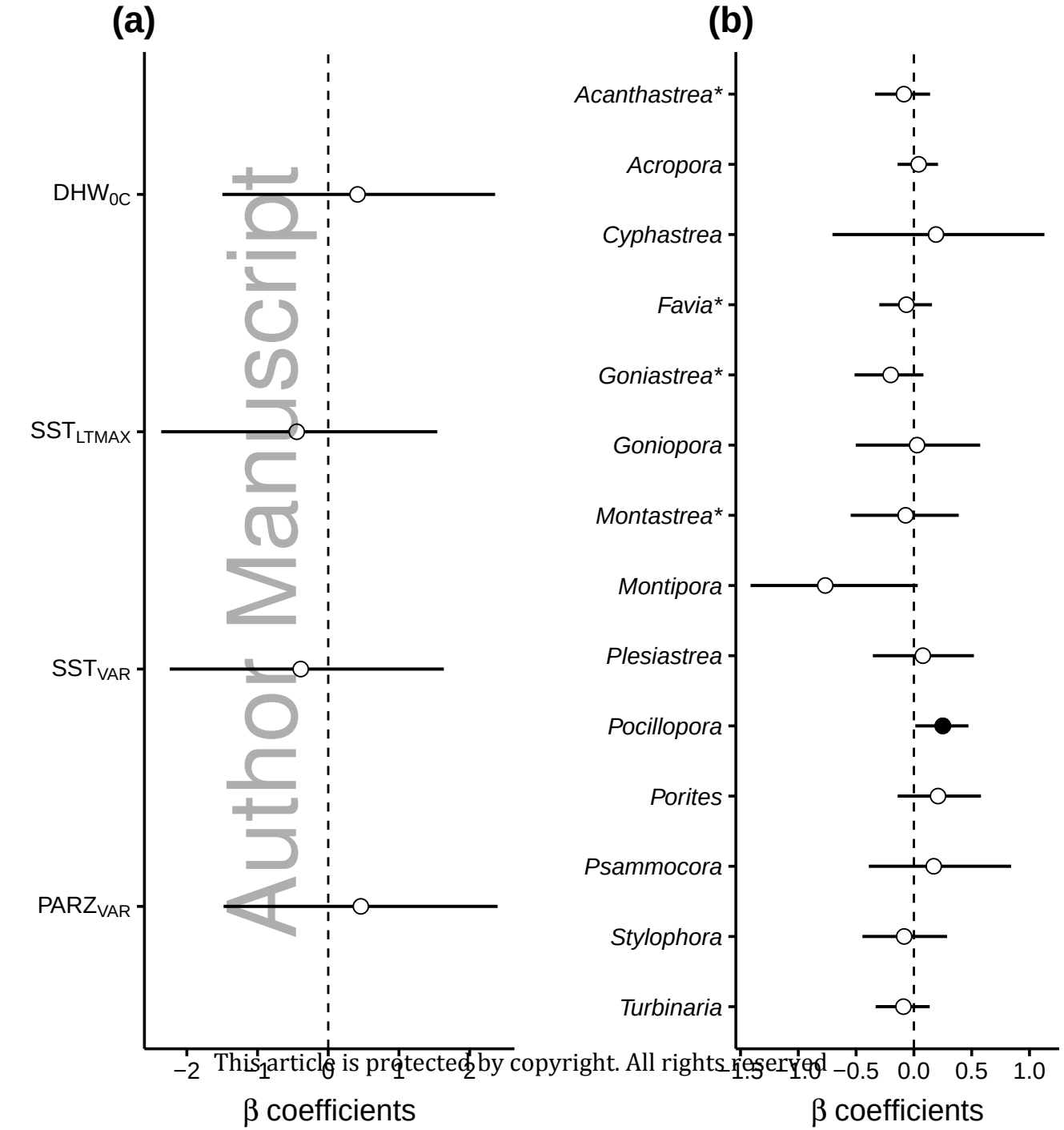

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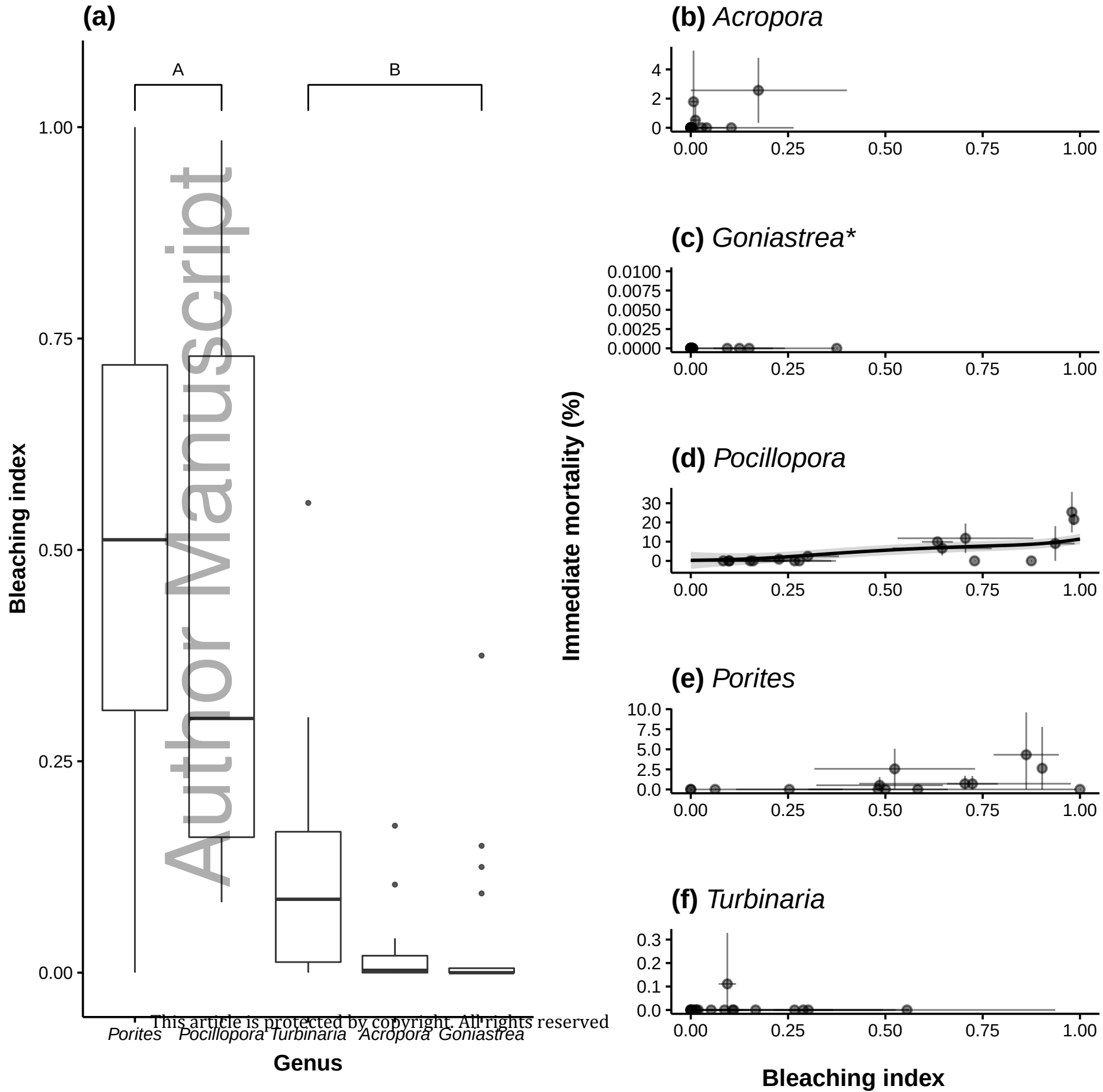

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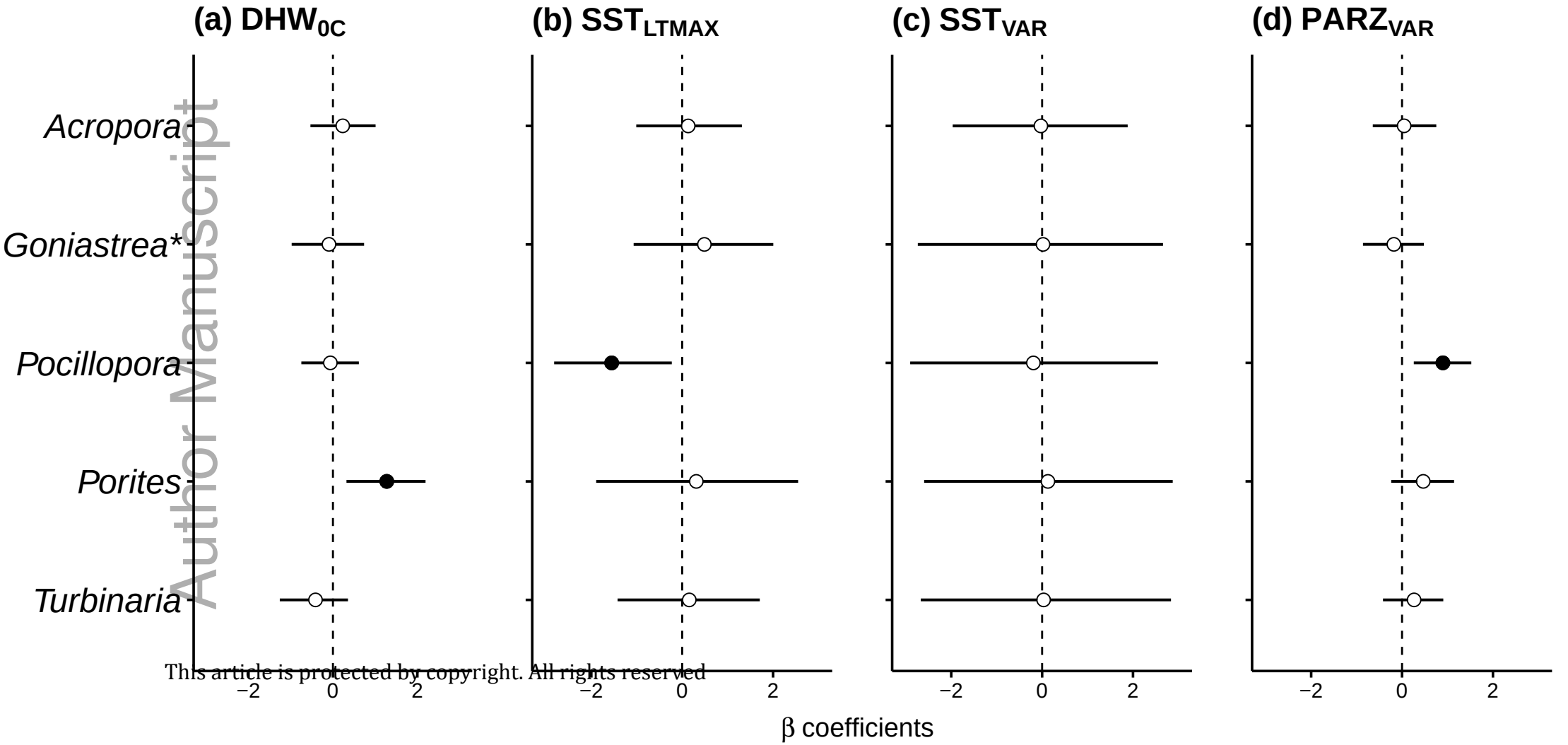

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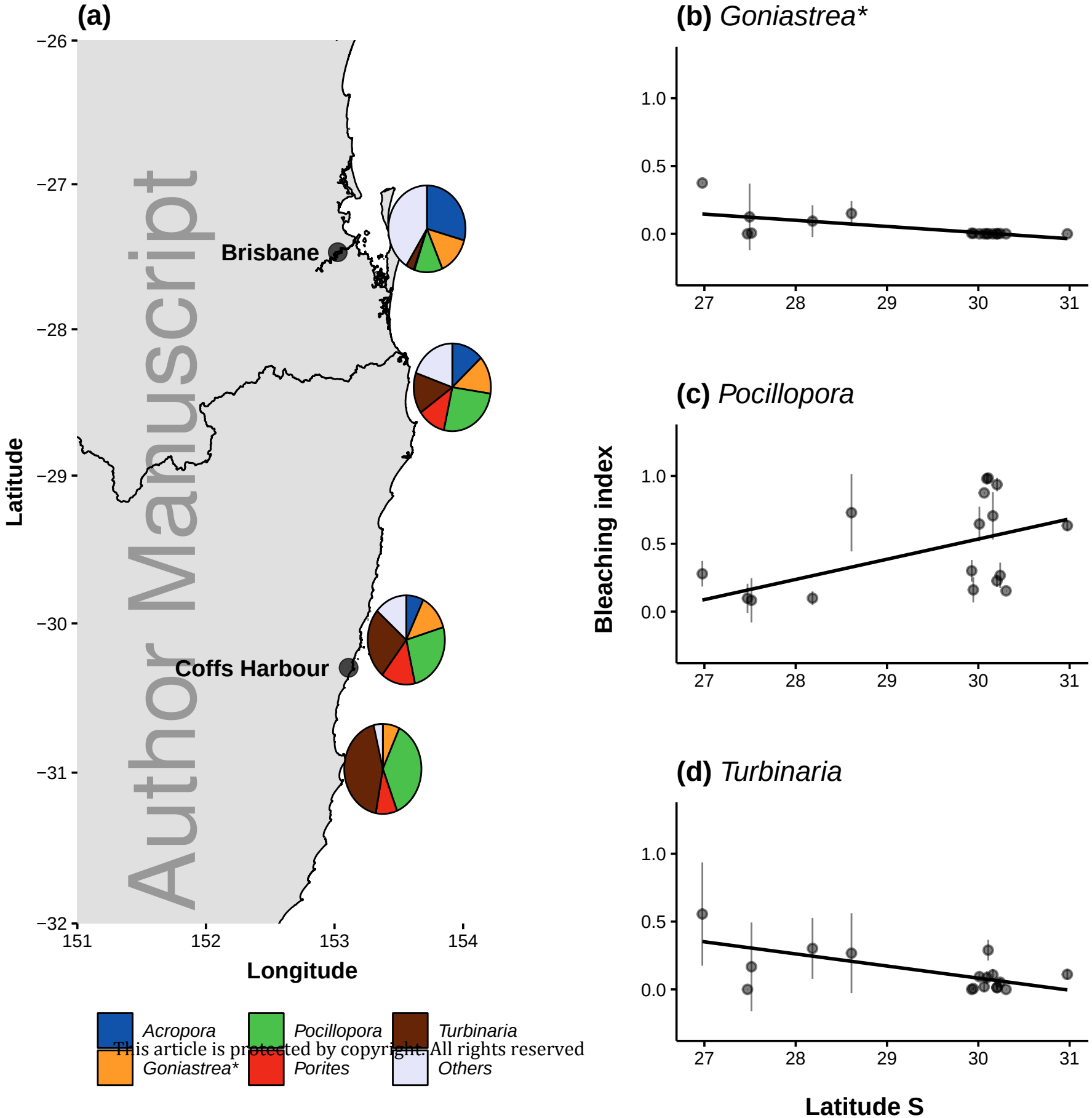

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